Nervous Rhythm arising from Rivalry of Antagonistic Reflexes: Reflex Stepping as Outcome of Double Reciprocal Innervation.

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I.

The observations with which the present communication deals were met with in experiments continuing those on reciprocal innervation of symmetrical muscles. In my previous paper on that subject* it had been reported that in regard to symmetrical extensors of the knee the ratio borne by intensity of the ipsilateral inhibition to the contralateral excitation is such that with equal stimuli to right and left symmetrical afferent nerves there is inhibitory suppression of contraction in both the muscles. In other words, under double reciprocal innervation the ipsilateral inhibition by each nerve completely overcomes the contralateral excitation of the other. It was shown that this mutual suppression holds over a wide range of the scale of intensities of stimulation. It was also shown that with quite weak stimuli a simultaneous stimulation of both nerves, stimuli being equal in intensity, often results in concurrent contraction of both muscles. Indeed, with quite weak stimuli, the effect of stimulation of each afferent nerve by itself is, in the decerebrate preparation, usually contraction of the ipsilateral as well as of the contralateral muscle.

This being so, it is evident that at some point in the scale of intensities of stimulation there should be a place below which contralateral excitation is stronger than ipsilateral inhibition, whereas above it ipsilateral inhibition is stronger than contralateral excitation.

My further experiments were directed to finding where on the intensities-scale this point actually lies. In prosecuting this search there began to be met instances of rhythmic contraction of exceedingly pronounced character.

Method employed.

The mode of preparation when the knee extensor was observed was as follows:—The animal (cat) was decerebrated under deep chloroform and ether narcosis. In both limbs all muscles were then detached from the great and lesser trochanters and intertrochanteric line. The insertions of right and left iliopsoas, psoas parvus, and tensor fasciæ femoris were then carefully resected up, and the origin of rectus femoris right and left. In both limbs the following nerves were severed: popliteal, small sciatic, hamstring, external cutaneous, obturator, internal saphenous and branch to the sartorius and pectineus. The peroneal of each limb was ligated tightly at its entrance into tibialis anticus just below knee. This procedure leaves the vastocrureus muscle of each limb the muscle operative in or on the limb. A steel drill in the condylar end of each femur is clamped to a heavy upright in such a position that, the preparation being supine, the two femora are nearly vertical and are parallel, and both hips are flexed to about a right angle. The root of the tail is fixed to the table by a steel pin. The leg is removed one-third down the tibia, and into the free end of that bone a fine steel pin is set; to this the thread attached to the myograph lever is fastened. The angle made by the tibia with the thigh varies with the degree of contraction of vastocrureus, and, the preparation being decerebrate, that muscle exhibits tonus, *i.e.* maintains the standing posture.

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* *Supra*, p. 219.

The resistance to the contraction of each vastocrureus was provided by the weight of the remaining portion of the limb below the knee and the adjustable tension of a light coiled wire spring attached to the lever of the myograph near its axis. The resistance was made as nearly similar as possible for both the right and the left muscle. The peroneal nerve on each side was stimulated with platinum electrodes, 4 mm. apart and placed with the nerve-trunk obliquely between them. The pair of electrodes was inserted sidewise through a glass tubulure in the wall of a glass tube, in which lay the ligated nerve itself. The muscles and skin around and over the electrode and tube were brought together and stitched. For flexor observations the psoas and tensor fasciæ femoris were employed and isolated, the animal being prone.

For stimulation a pair of similar Leeds induction coils were used, one for the right nerve, the other for the left. In the secondary circuit of each a resistance box of 100,000 ohms was introduced. A double switch connected to the circuits for both nerves allowed the coils to be interchanged for the two nerves at will, furnishing some opportunity of testing the approximate equality of the two circuits and of the relative excitability of the two nerves.

The right and left vastocrurei, thus completely isolated in each limb, but retaining blood and nerve supply and natural attachments quite intact, form a symmetrical pair of extensor muscles. Under the reflex action of, for instance, an afferent nerve of either limb, reciprocal innervation obtains for them as it does for an antagonistic muscle-pair. As shown, the afferent of each limb relaxes the ipsilateral vastocrureus by reflex inhibition, and causes the contralateral to contract by reflex excitation. The motor centre of the contralateral extensor reacts therefore to the afferent in the same direction as does that of the flexor of an ipsilateral antagonistic pair.

For the observations on double reciprocal innervation required I employed symmetrical afferent nerves, usually the peroneals, sometimes the popliteals. With simultaneous stimulation of both right and left nerves algebraic summation of the excitatory and inhibitory effects is of course the result.[*] Over a certain range of combinations this summation is readily observable because it results in contractions not wholly suppressed but of various grades of submaximal intensity. Somewhere within this restricted range of combinations of the opposed stimuli should lie the neutral point sought for in my experiments. When pursuing adjustments of the stimuli in order to arrive at determination of this it was found that rhythmic alternating contraction and relaxation, reciprocal in direction in the two muscles, appeared directly both stimuli were employed concurrently, though quite absent under either stimulus alone.

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[*] *Vide supra*, p. 226.

During these rhythmic reactions a glance at the preparation was enough to show that, although only the one thigh muscle remained in each limb, the animal was stepping with both limbs, usually at a quick walking pace, and whether the muscle remaining were an extensor or a flexor. It began to step as soon as ever the two antagonistic stimuli were concurrently combined, and it ceased to step directly their union was dissolved. Fig. 1 exemplifies this. There it is seen that it did not matter whether the combination were made by adding the inhibitory stimulus to the excitatory already in action, or the excitatory to the previously-acting inhibitory; in either case the stepping did not occur under either stimulus acting alone, yet ensued directly the two opposed stimuli were in action together. Conversely, on withdrawing either of the stimuli and leaving the other one in operation the stepping immediately ceased, each limb then passing into either steady contraction or steady relaxation, according as the remaining stimulus was contralateral to it or ipsilateral.

II.

Nervous inhibition seems in many ways the exact opposite and counterpart of nervous excitation. And since the process of nervous excitation is certainly rhythmic, its natural rhythm in mammalian motoneurones being probably about 50 impulses per second (Piper),[*] it may be argued that the process of nervous inhibition is probably similarly rhythmic. Yet in comparison with the slow periods of many rhythmic muscular acts, for instance those of breathing and stepping, a rhythmic frequency of 50 per second can be considered as tantamount to continuous and steady operation. It is a question how there are developed from such minutely oscillatory nervous discharge those coarser rhythmic actions with periods recurring once in 3 secs. as in breathing, or once a second as in the step, or four times a second as in the scratch reflex. The suggestion has often been made that such rhythmic nervous actions are the result of the concurrent action of two opposed nervous forces, the outcome of a constant opposition or resistance acting against a constantly discharging nervous activity. "How can the constant motion of the nervous fluid be changed to a periodic motion? When a conductor of electricity is held at some distance from the electric

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[*] 'Elektrophysiologie menschlicher Muskeln,' Berlin, 1912.

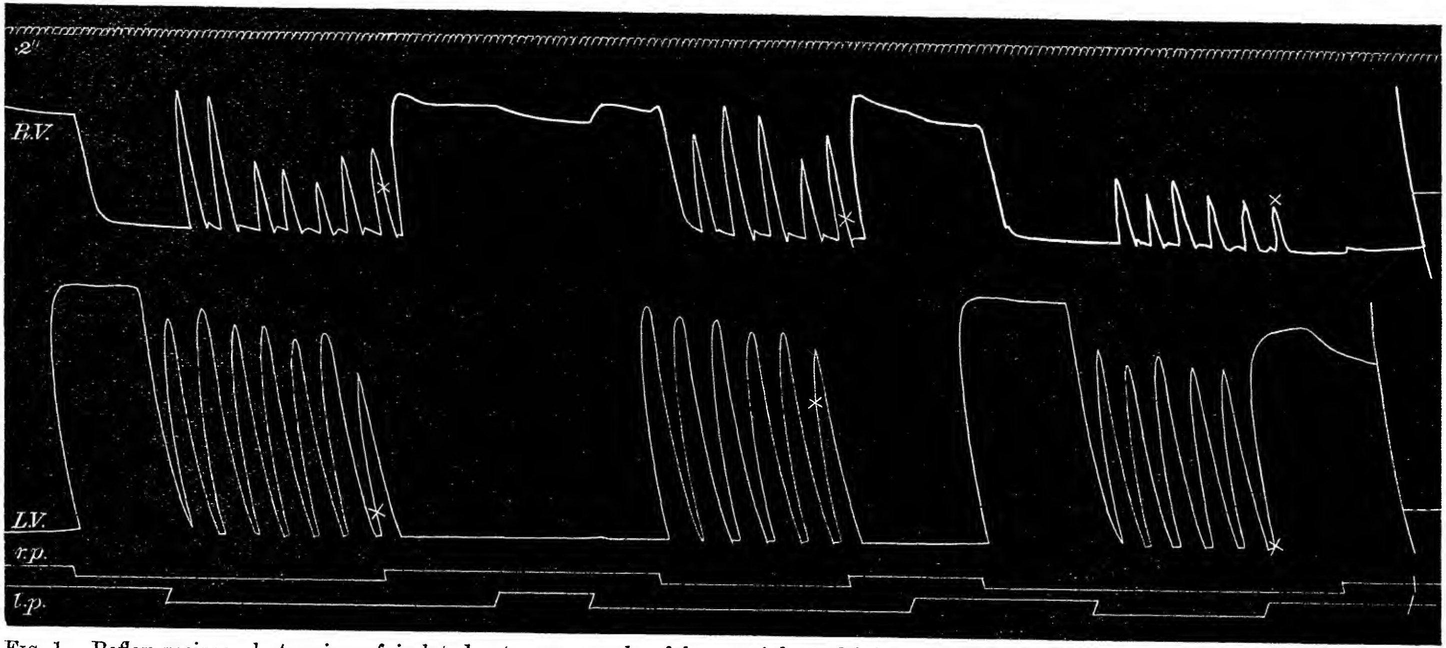

Fig. 1.—Reflex reciprocal stepping of isolated extensor muscle of knees, right and left, evoked by concurrent stimulation of the antagonistic nerve-pair, right peroneal (*r.p.*) and left peroneal (*l.p.*) used as afferents. Decerebrate cat. R.V., right vastocrureus muscle; L.V., left vastocrureus muscle. Time in fifths of seconds above. The small crosses mark the moments at which the combination of inhibitory and excitatory stimulation is broken by withdrawal of one or the other. Ascent of myograph line denotes contraction, descent relaxation. The preparation is a tonic one, so that descent of myogram line means active inhibitory relaxation. Further explanation given in text, p. 241.

machine, kept in a state of constant excitement, the electricity is given off periodically. The dry air between the machine and the conductor held near it impedes progress of the electricity to the conducting body until the electricity accumulates in quantity to overcome the impediment offered in its course, and the electricity escapes in a succession of sparks. This is an illustration of how the current of the nervous principle may be rendered periodic."* A well-known application of this explanation to a particular case of nervous rhythm was that given by Rosenthal† for the inhibitory action of the superior laryngeal on the respiratory centre (1862). He concluded that the stream of nervous impulses from the constantly discharging and blood-stimulated respiratory centre meets a resistance to its outflow and thereby becomes rhythmic, much as does a stream of air passing out from a tube under water (*op. cit.*, p. 242). He described the function of the superior laryngeal nerve as being to increase this resistance and thus slow and deepen the respiratory movements; and the function of the rest of the vagus as being to lessen the resistance and thus render the respiratory rhythm less deep and more frequent. He argued that other inhibitory nerves act on their respective mechanisms in the same manner as does the superior laryngeal on the respiratory centre.

When a skeletal muscle's reflex contraction is partly antagonised by a reflex inhibition insufficient to suppress it entirely, the contraction thus moderated by inhibition often shows oscillations. A. Forbes‡ has put the question whether these oscillations may not mean that nerve-impulses constantly generated by the reflex excitatory nerve break through the inhibitory resistance periodically, just as, on Rosenthal's view, do the inspiratory impulses from the respiratory centre.

Undulations tend commonly to appear in reflex contractions obtained under concurrent reflex excitation and inhibition,§ and both T. Graham Brown|| and Forbes¶ have independently called attention to features in them. Of such undulations two main forms may be distinguished, and it seems at present well to regard the two separately, although the same principle of production may underlie both.

In one form, the undulations are smaller, more rapid, less regular, and

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* John Müller, 'Handb. d. Physiol.,' 1835, vol. 11, p. 77.

† 'Die Athembewegungen u. ihre Beziehungen zum Nervus Vagus,' Berlin, 1862.

‡ 'Roy. Soc. Proc.,' July, 1912, B, vol. 85, p. 289.

§ 'Roy. Soc. Proc.,' 1909, B, vol. 81, p. 268; *cf.* also 'Quart. Journ. Exper. Physiol.,' 1908, vol. 1, p. 7.

|| 'Roy. Soc. Proc.,' 1912, B, vol. 85, p. 278.

¶ *Ibid.*

have a frequency of about 8–10[*] or 7–12 per second.[†] Figures showing this form have been furnished in previous papers in these 'Proceedings.'[‡] The oscillations are often compounded into or with slower ones so that the graphic records show compound waves.

In the other form the undulations are slower and often of much more regular rhythm and amplitude than the above. As seen in figures furnished in these 'Proceedings,' by T. Graham Brown,[§] they show on the muscle contraction as notches or teeth in series from three to seven in number, each undulation lasting not far short of a second. Forbes figures[‖] a remarkable example with oscillations more ample, less regular, proceeding through a long series with a rate often of about 1 per second.

In a paper of my own an example of this slower form of undulations was figured,[¶] recorded simultaneously in flexor and extensor muscles of the knee; it was there (p. 268) pointed out that these undulations are reciprocal in sense in the antagonistic muscles, puffs, so to say, of inhibition in the one muscle's centre corresponding with puffs of excitation in the other's. Graham Brown,[**] observing the antagonist muscles of the ankle, notes also there that where (fig. 3 of his paper) the undulations were visible in both the antagonists they were reciprocal in them.

An important suggestion is made by Graham Brown, namely, that these slower undulations are "akin to the rhythmic act of progression."[††] This suggestion the results given in the present pages leave no room to doubt is correct. Graham Brown believes "that the rhythmic phenomenon is conditioned by a balance of" "activities which produce in the same centre equal and opposite effects (excitation and inhibition)."[‡‡] Forbes,[§§] referring to the less regular and less orderly oscillations met in his experiments, writes: "Perhaps all" these oscillations "are manifestations of a general tendency of opposed influences in reflex centres, although themselves continuous, to produce rhythmic activity. If so, it is conceivable that some conditions of intensity or time relations produce the regular movements of progression by enabling the centres to fall into a rhythm natural to them, whereas other conditions . . . just miss the natural rhythm of the centres and produce a confused rhythm instead."

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[*] Forbes, *ibid.*, p. 293.

[†] *Cf.* 'Quart. Journ. Exper. Physiol.,' *loc. cit.*, p. 74, fig. 6.

[‡] Forbes, 'Roy. Soc. Proc.,' B, vol. 85, pp. 293, 297, figs. 3, 4; Sherrington, *ibid.*, B, vol. 80, pp. 569–574, figs. 1–4; *ibid.*, B, vol. 81, pp. 250, 262, figs. 1, 10.

[§] 'Roy. Soc. Proc.,' 1912, B, vol. 85, pp. 281–283, figs. 1, 2, 3.

[‖] 'Roy. Soc. Proc.,' 1912, B, vol. 85, p. 292, fig. 1.

[¶] 'Roy. Soc. Proc.,' 1909, B, vol. 81, p. 261, fig. 9, B.

[**] 'Roy. Soc. Proc.,' *loc. cit.*

[††] *Ibid.*

[‡‡] *Ibid.*, p. 287.

[§§] 'Roy. Soc. Proc.,' *op. cit*, p. 297.

In conformity with this opinion the discrete and regular contractions shown in fig. 1, presenting the appearance of a rhythmic series of wholly separate contractions, which are reciprocals of similar complete relaxations in the fellow muscle, are in reality examples of the above discussed slow form of undulation incident to reflex contraction under concurrent inhibition and

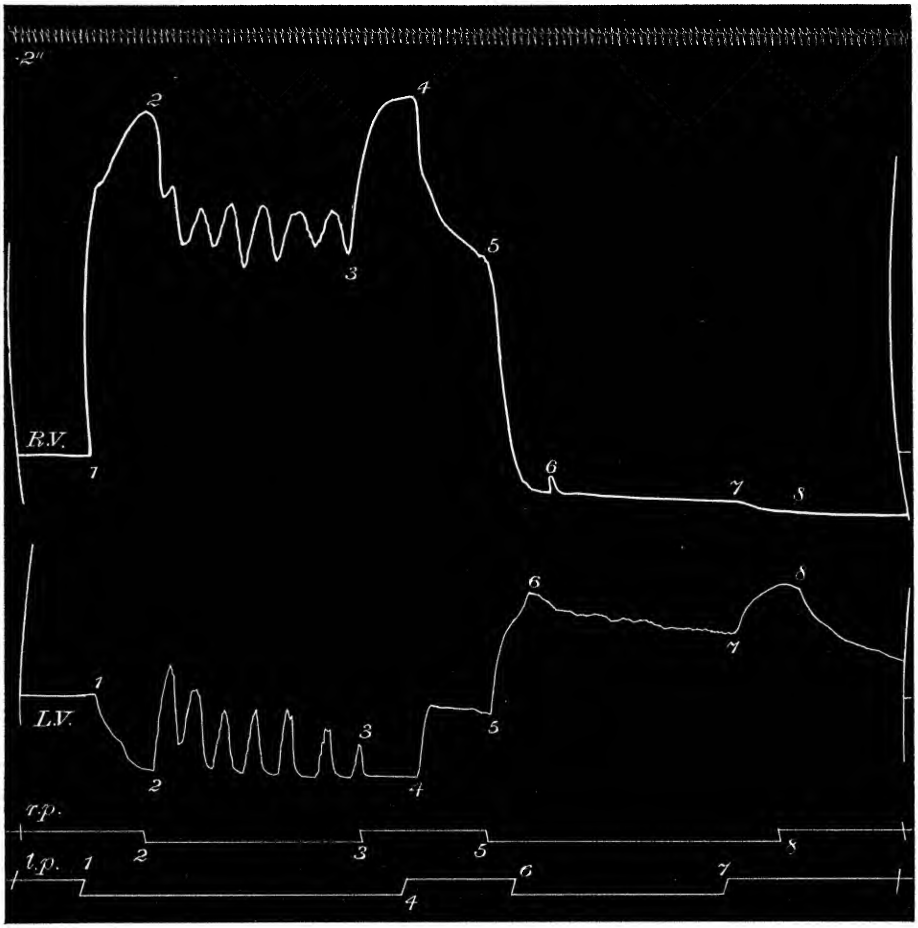

Fig. 2.—Reciprocal stepping of isolated extensor muscle of knees, right and left, reflexly evoked by concurrent stimulation of the antagonistic afferent nerves *l.p.*, left peroneal, and *r.p.*, right peroneal. Decerebrate cat. R.V., right vastocrureus; L.V., left vastocrureus. Correspondences between the stimulation signals and the myograph events indicated by numerals. The right peroneal stimulation following the left produces the rhythmic though somewhat imperfect stepping, but the left following the right, although the same physical stimuli are employed, fails to do so. Time above in fifths of seconds.

excitation; examples, it is true, in which the regularity and amplitude of rhythmic contraction and relaxation have reached their full. That these rhythmic contractions are really analogous to the simple undulatory reflex contractions cited and discussed above seems clear from several considerations. (1) Both occur under the same circumstance, namely, concurrence of inhibition and excitation. (2) Both exhibit the same rate of rhythm. (3) It has not been difficult in my experiments to find intermediate examples connecting the more developed forms with the less developed. Thus, the example fig. 2 is intermediate between the form exhibited by fig. 1, and the example figured in observation A, fig. 6; and the example fig. 3 seems to me intermediate between that of fig. 1 and the example figured by Forbes

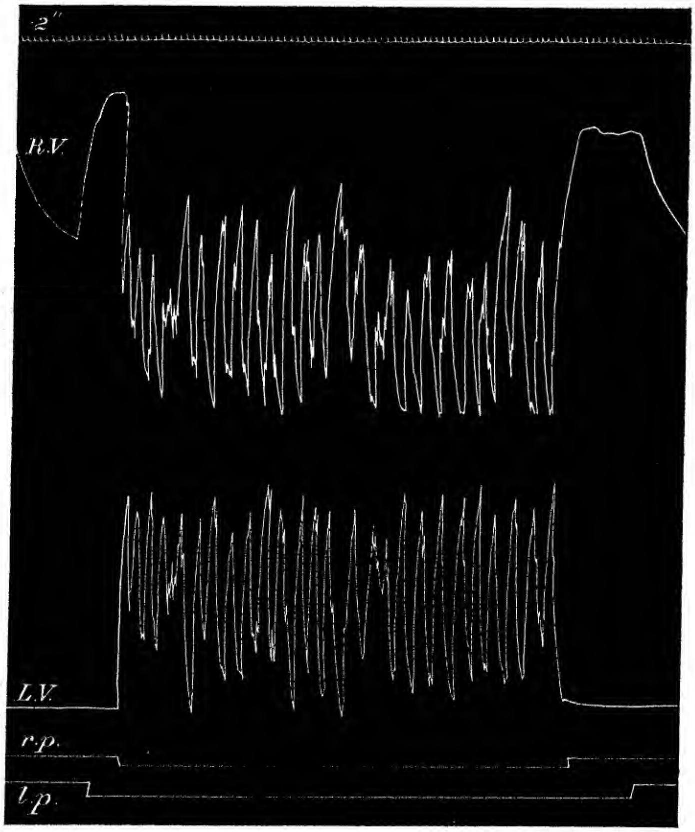

Fig. 3.—Reflex reciprocal stepping of isolated extensor muscle of knees, right and left, evoked by concurrent stimulation of the antagonistic afferents *r.p.*, right peroneal, and *l.p.*, left peroneal. Decerebrate cat. R.V., right vastocrureus muscle; L.V., left fellow muscle. Time above in fifths of seconds. In addition to the rhythmic stepping, which is here somewhat rapid, there is a minute tremor of much more rapid rate (see text) engrafted on and disturbing the stepping reflex's rhythm.

(*op. cit.*, fig. 1). By varying the conditions of experiment various transitional forms can be obtained between imperfect irregular rhythmic movement and the complete regular rhythmic series of movements constituting stepping. Figs. 6, 7, and 15 furnish some illustration of this.

III.

Turning now to analyse some of the features of the rhythmic stepping the example in fig. 1 may be used. The observation begins with stimulation (faradic) of the right peroneal nerve, causing immediate inhibitory reflex relaxation of the right knee extensor with synchronous reflex contraction of the left fellow muscle; both relaxation and contraction are perfectly steady and arhythmic. After 2·5 secs., during which time the left muscle has remained perfectly steadily relaxed and the right perfectly steadily contracted, stimulation (faradic) of the left peroneal nerve is commenced, that of the right still continuing unchanged. The steady relaxed condition of the right muscle is at once broken by a contraction and at the same moment the steady contracted condition of the left muscle is broken by an inhibitory relaxation. The r. contraction and the l. relaxation culminate synchronously in about 0·4 sec., and then die out about as rapidly as they appeared, to reappear and similarly culminate synchronously again. In this way they rhythmically and reciprocally appear and reappear in series so long as the concurrent stimulation of the two nerves right and left is kept up, namely, for 6·5 secs., seven complete steps being taken in that time by the extensor muscle of each knee. The r. stimulus, the one commenced with, was then withdrawn. The stepping immediately ceases in each muscle, except that the r. muscle, which, having begun its stepping by contraction, is at the end of the seventh step, relaxes, carries out a half-step more and passes into steady contraction, thus assuming an attitude of full extension of knee; and that similarly the l. muscle, which, having begun with relaxation, is at the end of seventh step, contracts, executes a half-step more, passing into relaxation and assuming a posture of flexion of knee. These final half-steps and assumptions of reciprocal states at the two knees are, of course, due to the action of the stimulation of the left nerve now remaining unopposed by any concurrent stimulation of the antagonist right nerve. The l. nerve stimulation remains in operation until withdrawn 3·5 secs. later. During its sole action no trace of rhythm appears in either muscle. On its withdrawal the contraction of right muscle at once begins to decline, although, the preparation being the tonic one, the "shortening reaction" of "plastic tonus" has taken place, and the tonic shortness of the muscle still persists after withdrawal of the stimulus. In the left muscle on withdrawal of left nerve stimulus no obvious change occurs, because the stimulus is inhibitory and under it the muscle is already relaxed and relaxes no further and no less on cessation of the excitation, a "lengthening reaction" having occurred at end of the r. nerve stimulation.

Three seconds later the left nerve stimulation is recommenced; steady contraction of r. muscle is reassumed; l. muscle being already relaxed the inhibitory effect there is not apparent, although really fully existent, as subsequent events show. The l. nerve stimulus is here the pre-current stimulus, and under it no rhythm of any kind appears in either muscle any more than did under r. nerve stimulus in the preceding observation. But on then applying stimulation of r. nerve, that of l. still continuing as before, rhythmic stepping at once appears. It begins synchronously in right and left muscles, the opening phase being contraction, *i.e.* extension of limb, in the left muscle, and relaxation, *i.e.* flexion of limb, in the right muscle. On withdrawing the r. nerve stimulus, about 6 secs. later, when the last step of a sequence of six has been nearly completed, the stepping ceases abruptly with completion of that step. The right muscle then reverts to steady contraction, the left to full relaxation. This resumption is, of course, the effect of the still-continuing l. nerve stimulation, and guarantees that the stimulation of that nerve has remained effective throughout. Rather more than a couple of seconds later the l. nerve stimulation is withdrawn and the contraction of right muscle, in consequence, shows decline, modified, however, by the shortening reaction of the plastic tonus.

Two seconds later r. nerve's stimulation is once more commenced. It evokes steady contraction of l. muscle and, synchronously with that, full inhibitory relaxation of r. muscle. During the 3·5 secs. for which this stimulus remains thus in operation by itself, the steady reciprocal reaction of the two muscles is maintained unchanged. The stimulation of l. nerve is then commenced, that of r. nerve continuing unaltered. Synchronous stepping, reciprocal in direction in the two muscles, sets in at once. Here the opening phase in each muscle is the reverse of that in the previous observation. The l. nerve stimulus is maintained in concurrence with that of r. nerve for 7 secs., and during that period a sequence of six complete and regular steps is performed by each muscle. Stimulation of l. nerve is then withdrawn, and both muscles at once revert to the non-rhythmic steady state they exhibited previously under stimulation of r. nerve alone, r. muscle being in steady relaxed condition, and l. muscle held steadily contracted. Later, the stimulation of r. nerve is itself finally withdrawn; the contraction of l. muscle then at once begins to decline into pure statotonus, and r. muscle shows a slight return to greater tone than it had during the influence of r. nerve's stimulation.

Although the results, therefore, appear curiously simple, the conditions underlying them are a complex of various factors. Without pretending to offer any full analysis of these, some of them may be here briefly adverted to.

1. *Influence of the Laterality of the Stimulus.*

Decisive points here are (1) that reciprocal innervation holds for the symmetrical muscles, (2) that with extensors the direction of reciprocity is excitation contralateral and inhibition ipsilateral, with flexors conversely, and (3) that the rhythmic stepping here concerned arises, proceeds, and ceases with commencement, continuance, and withdrawal of the exercise of double reciprocal innervation.

In such observations as shown in figs. 1, 4, and 9, we may term the stimuli according to their sequence "pre-current," "added," and "remaining." It will be seen from the figures that the added stimulus when extensor muscles are used always causes, as its first effect, the contraction phase of the contralateral muscle's reaction, and the relaxation phase of the ipsilateral muscle's reaction. That is, it causes, as its first effect, the extension phase of the step at the contralateral knee and the flexion phase of the step at the ipsilateral knee. This is in agreement with the rule observed in the case of stepping provoked by direct faradisation of the spinal cord. As noted previously,* I found that regular stepping of the hind limbs is readily provoked in the spinal animal by unipolar faradisation applied with a stigmatic electrode directly to a certain area of the distal cut face of the cord in the cervical region. If the electrode be applied in the right lateral half of the cord the stepping begins with flexion phase of right hind limb, and extension phase of step in left hind limb.

It might have been supposed that the reflex stepping produced by the double reciprocal action of symmetrical r. and l. afferents upon the knees r. and l. symmetrical extensor muscles must of necessity be bilateral. Experiment shows, however, that that is, in fact, not the case. The reflex stepping so obtained, although usually bilateral, is sometimes unilateral. Thus, figs. 4 and 5 are from the same experiment at short interval. In the former the stepping is bilateral, in the latter it is confined to the left muscle. The observation in fig. 4 was obtained with values of stimuli right nerve 15 cm. left nerve 17 cm. as measured on scale distances of the two induction apparatus.

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* 'Journ. Physiol.,' 1910, vol. 40, p. 86; 'Brain,' 1910, vol. 33, p. 13; also Roaf and Sherrington, 'Quart. Journ. Exper. Physiol.,' vol. 3, p. 210; and G. Brown and Sherrington, *ibid.*, vol. 4, p. 202.

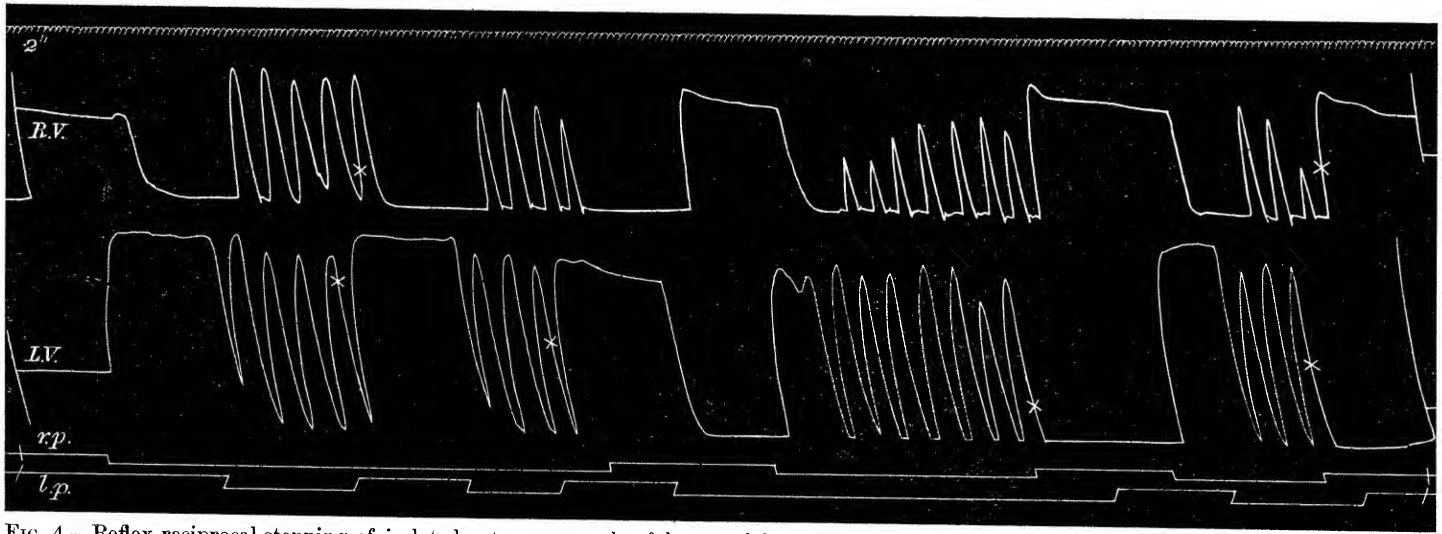

Fig. 4.—Reflex reciprocal stepping of isolated extensor muscle of knees, right and left, evoked by concurrent stimulation (faradisation) of the antagonistic afferents *r.p.*, right peroneal, and *l.p.*, left peroneal. R.V., right vastocrureus muscle; L.V., left vastocrureus muscle. Time above in fifths of seconds. Crosses mark moment of withdrawal of the concurrent stimulus. Stimulus values $\frac{\text{r.p. 15 cm.}}{\text{l.p. 17 cm.}}$. Further description in text, p. 243. From same experiment as fig. 5.

The threshold stimulus for r. nerve had been found slightly higher than that for left in this preparation; the two stimuli although not equal (as shown later *v. infra*) were certainly not far from equal. Then, for obtaining observation, fig. 5, the r. nerve stimulus was increased to 13 cm. and l. nerve stimulus to 16 cm. Both stimuli were therefore increased, but that of r. nerve much more than that of l. nerve, the steepness of ascending intensity of the physical stimulus being much greater between 15 cm. and 13 cm. than between 17 cm and 16 cm. of the scale. This unequal increase of intensity of stimulation of the two nerves r. and l. is answerable for the change from bilateral stepping to unilateral. It suppresses the stepping in the muscle on the same side as the stronger stimulus, and at the same time makes the stepping of the other, the left, muscle faster than it was in fig. 4. It brings this about in the following way. With increase of the strength of the stimulus its ipsilateral inhibition increases more than does its contralateral excitatory effect. When (fig. 4) r. stimulus has a value of 15 cm. it does not suppress the contralateral excitatory effects of l. stimulus at value 17 cm., but

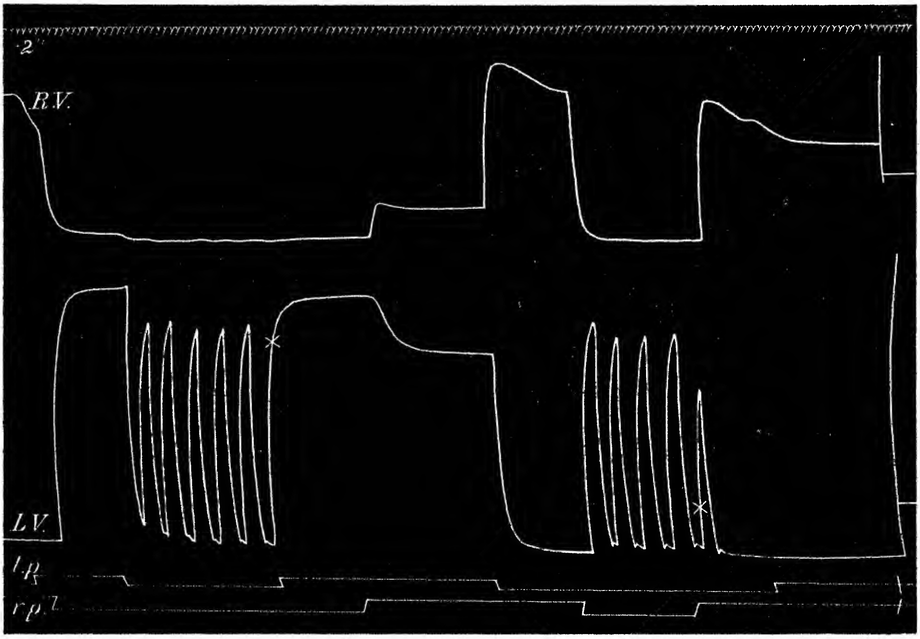

Fig. 5.—Reflex unilateral stepping as exhibited in an isolated extensor muscle of left knee, the similarly isolated extensor of right knee being relaxed by inhibition while the fellow muscle steps. Decerebrate cat. From same experiment as fig. 4, but with different combined stimulus value, namely $\frac{\text{r.p. 13 cm.}}{\text{l.p. 16 cm.}}$. *r.p.* and *l.p.*, right and left peroneal nerves. Time above in fifths of seconds. Further explanation in text, p. 245.

r. at value 13 does suppress all contralateral excitatory effects from l. at value 16. The r. muscle therefore in fig. 5 does not step. But in the l. muscle l.'s stimulus value 16 restrains the contralateral excitatory effects of r.'s stimulus value 13 even less than was the case when l.'s stimulus was value 17 and r's stimulus value was 16. Hence the l. muscle steps faster in fig. 5 than in fig. 4, r.'s excitatory effect breaking through l.'s inhibition more rapidly and frequently. This quickening of the step under the stronger stimulus harmonises with the observation that though the direct faradisation required to excite stepping from a point in the cross-section of the cervical spinal cord is of quite weak intensity, the rate of the stepping of hind limb so produced increases, *ceteris paribus,* with the intensity of the faradic stimulus.

2. *Strength of Stimulus.*

As to the strength of the antagonistic stimuli which by their concurrence evoke the stepping, the phenomenon, in my experience, is not obtainable with strong stimuli. With stimuli just above threshold intensity I have at times seen traces of the rhythmic undulation; but attempts to develop it with such very weak stimuli have not so far attained much result. Stimuli rather stronger than such but on the weak side of moderate have yielded the best results. Weakening the stimuli beyond that point gives a rhythm not only slower but more irregular with waves of varying amplitude (fig. 6A), and a tendency to pauses between some of the beats. On the other hand, with too strong stimuli there is a tendency for the rhythmic reaction to be suppressed in one or other member of the muscle-pair, and for it to be represented in the other member by a few sharp somewhat irregularly explosive beats separated by longish unequal intervals (fig. 6B). An idea of the range of intensities suitable may be afforded by the data of an experiment. In the experiment from which figs. 6A and 6B, and also fig. 4, have been taken, the threshold value for reflex effect both ipsilateral and contralateral lay for r. nerve at 17·8 cm. and for l. nerve at 19·2 cm. This seems high, but it must be remembered that a resistance box of 100,000 ohms was included in each circuit. Slight but distinct rhythmic stepping was obtained by the combination r. at 16 cm. and l. at 18 cm. $\left(=\frac{\text{r. }16}{\text{l. }18}\right)$, fig. 6A. More regular and stronger rhythm was obtained with various stronger combinations, *e.g.*, $\frac{\text{r. }15}{\text{l. }17}$ (fig. 4), $\frac{\text{r. }14}{\text{l. }17}$, $\frac{\text{r. }13}{\text{l. }15}$. Results with $\frac{\text{r. }12{\cdot}5}{\text{l. }13{\cdot}5}$ were less good. A result with $\frac{\text{r. }11}{\text{l. }12{\cdot}5}$ is given in fig. 6B; it exhibits no stepping with right muscle, and merely two short unequal steps with left muscle in a period of concurrence of the stimuli covering more than 3 secs. With $\frac{\text{r. } 10{\cdot}5}{\text{l. } 12}$, and all stronger combinations tried, there was obtained no rhythmic stepping movement at all, although excellent steady contractions and inhibitions.

Weaker stimuli tend, in my experience, to give slower rhythm. Other factors in the production of the rhythm, for instance, the ratio between the strengths of the antagonistic stimuli, change, however, of necessity also in such comparisons. Still my facts, as far as they at present go, clearly indicate the above tendency. Thus figs. 4 and 6 are from the same experiment. In fig. 6A the stimuli were $\frac{\text{r. } 16}{\text{l. } 18}$, and the beats are 9 during 8·5 secs., while in fig. 4, observation 3, where the stimuli were $\frac{\text{r. } 14}{\text{l. } 17}$, the beats are 7 during 5·2 secs. Again fig. 7, observations A, B, and C are all

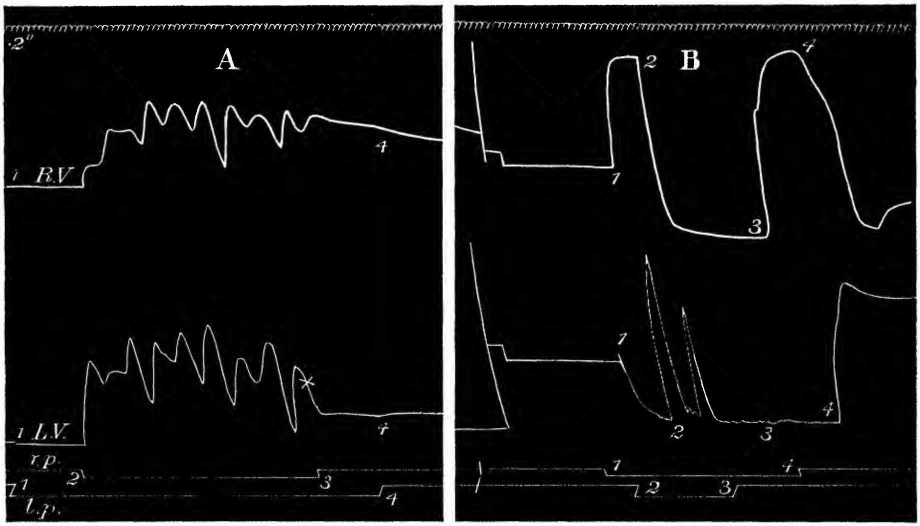

Fig. 6.—Reflex rhythm (imperfect stepping) evoked in the isolated extensor of knees, right and left, by concurrent stimulation of the antagonistic afferents, right and left peroneals, *r.p.* and *l.p.* Decerebrate cat. In Observation A the stimulus values are too weak $\frac{\text{r.p. } 16 \text{ cm.}}{\text{l.p. } 18 \text{ cm.}}$; in Observation B they are too strong $\frac{\text{r.p. } 11 \text{ cm.}}{\text{l.p. } 12{\cdot}5 \text{ cm.}}$; both observations are from the same experiment as fig. 4, where good and regular reflex stepping is obtained with stimulus values $\frac{\text{r.p. } 15 \text{ cm.}}{\text{l.p. } 17 \text{ cm.}}$. In Observation A it is noteworthy that the stimulation of *l.p.* is so weak that it of itself produces no obvious contraction of the contralateral muscle and only the merest trace of relaxation of the ipsilateral muscle. Yet its presence is documented at once when the concurrent stimulus is added in the response being then not steady but rhythmic. Further explanation in text, p. 246.

from one experiment. In fig. 7A the combined stimuli $\frac{\text{r. } 14}{\text{l. } 16}$ give five steps in 14 secs., but strengthening stimulus r. to 13, so that the combined stimuli become $\frac{\text{r. } 13}{\text{l. } 16}$, results (fig. 7B) in 13 steps during 17·5 secs., and strengthening both stimuli further still to $\frac{\text{r. } 12}{\text{l. } 13{\cdot}5}$ produces (fig. 7C) five steps during 3·8 secs.

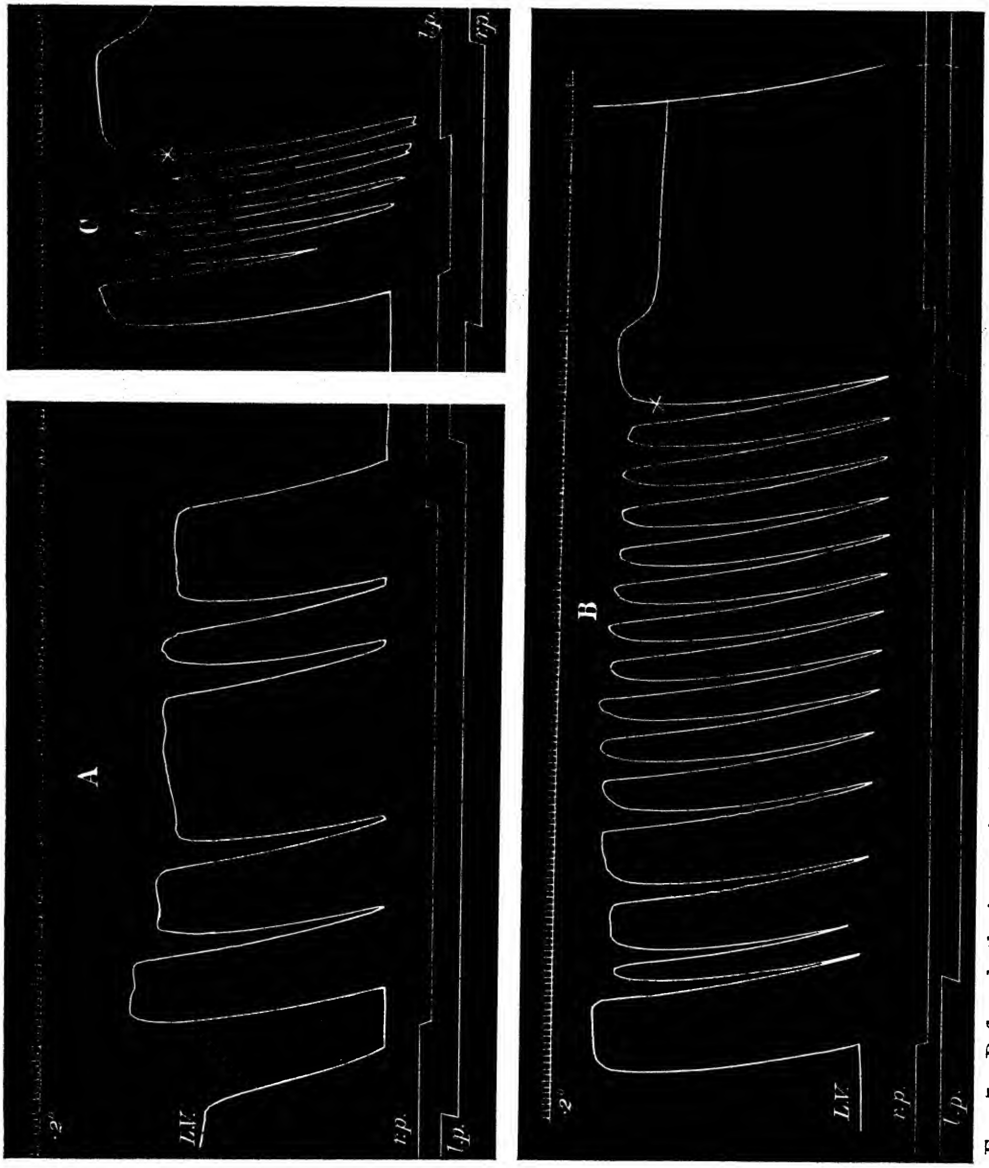

FIG. 7.—Reflex rhythmic stepping of isolated extensor muscle L.V. of left knee (decerebrate cat) evoked by concurrent stimulation of *r.p.*, right peroneal, and *l.p.*, left peroneal, nerves as afferents. Stimulus values for Observation A are $\frac{\text{r.p. } 14 \text{ cm.}}{\text{l.p. } 16 \text{ cm.}}$, for B are $\frac{\text{r.p. } 13 \text{ cm.}}{\text{l.p. } 16 \text{ cm.}}$, and for C are $\frac{\text{r.p. } 12 \text{ cm.}}{\text{l.p. } 13{\cdot}5 \text{ cm.}}$. Time above in fifths of seconds. Further explanation in text, p. 247.

More satisfactory for comparison is fig. 8 with fig. 5. Both are observations from the same experiment, with no long interval between them. The l. stimulus was of the same value in both, namely, 16 cm. But the r. stimulus had value 15·5 cm. in the observation fig. 8, whereas in that of fig. 5 its value was 13 cm. The results contrast in three striking features. Where r. stimulus is stronger (fig. 5) the rate of stepping is six double phases in 4·8 secs., as against four double phases in 4 secs., where r. stimulus is weaker. Where r. stimulus is weaker (fig. 8) the stepping is not so well maintained as where r. stimulus is stronger. Where r. stimulus is weaker (fig. 8) the stepping occurs in the fellow muscle of the right side as well as in the left, and where r. stimulus is stronger (fig. 5) the stepping is confined to the left-side muscle.

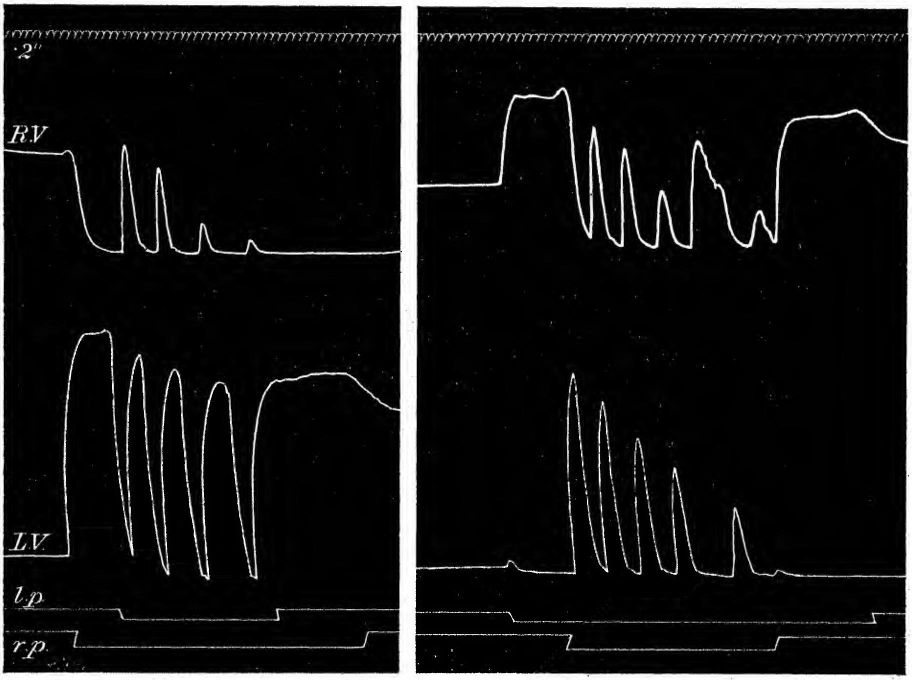

Fig. 8.—Reflex reciprocal stepping as exhibited by isolated extensor muscle of knees, right and left, evoked by concurrent stimulation of antagonistic afferents, right and left peroneals, *r.p.* and *l.p.* Decerebrate cat. Time above in fifths of seconds. Compare fig. 5. Explanation in text, p. 249. Stimulus value $\frac{\text{r.p. } 15{\cdot}5 \text{ cm.}}{\text{l.p. } 16 \text{ cm.}}$.

3. *Influence of Intensity-ratio between the two Antagonistic Stimuli.*

From the preceding section it is clear that as might be expected the proportion between the intensities of the two antagonist stimuli is an important factor in determining the existence and characters of the rhythmic reflex. Evidence of this was constantly met in the experiments. In fig. 7 the two observations A and B illustrate an aspect of it. Stepping is more marked in B than in A although the intensity of one only of the rival stimuli was altered. Conversely, the change of intensity by even a little of one of the antagonist stimuli may make all the difference to whether the combination be effective or not for rhythmic stepping. My experience put generally is

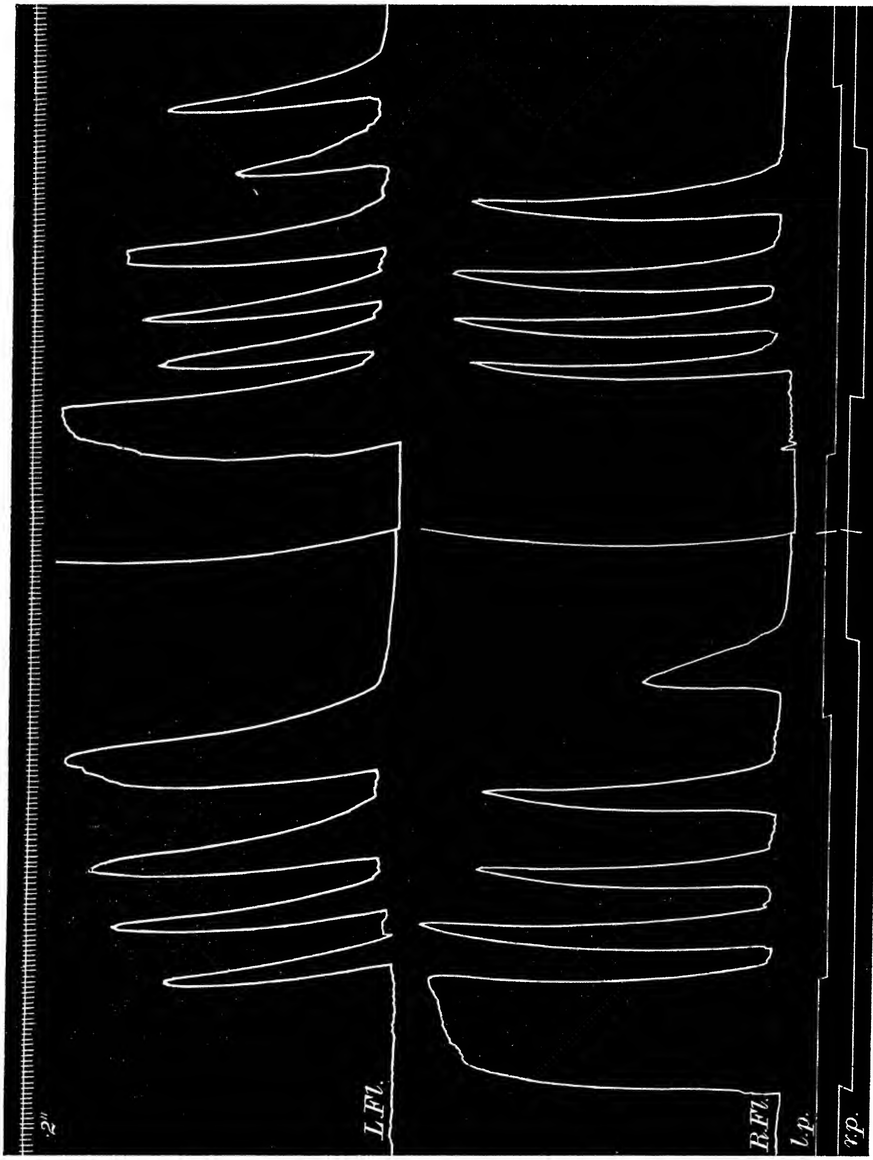

Fig. 9.—Reflex reciprocal stepping as exhibited by isolated flexor muscles, R.F., L.F., of hips, right and left, evoked by concurrent stimulation of right and left peroneal nerves, *r.p.* and *l.p.* The direction of the reciprocal innervation is here contraction ipsilateral and inhibitory relaxation contralateral. Time above in fifths of seconds. Decerebrate cat. The muscles, both right and left, were psoas and tensor fasciæ femoris.

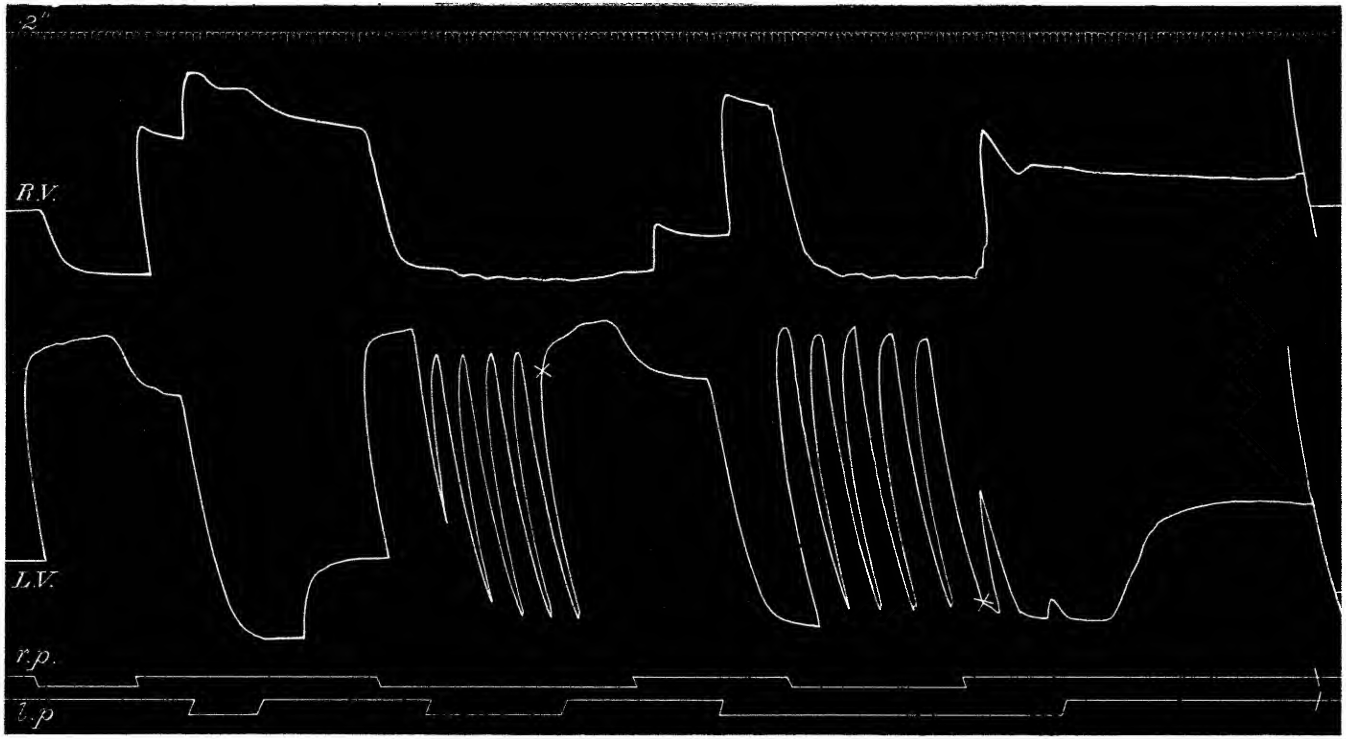

FIG. 10.—Reflex stepping induced in the isolated extensor muscle of the left knee, but not in that of the right, by concurrent stimulation of the antagonistic afferent nerves, *r.p.*, right peroneal, and *l.p.*, left peroneal. Decerebrate cat. R.V., right vastocrureus muscle; L.V., left vastocrureus muscle. Time above in fifths of seconds. Stimulus values $\frac{\text{r.p. 13 cm.}}{\text{l.p. 16 cm.}}$. The first two observations in the figure show the separate reactions of the two separate stimuli which, when concurrent, give the unilateral stepping of the two last observations of the figure. Further explanation in text, p. 252.

that the antagonist stimuli must not be very unequal in intensity if they are to provoke the rhythmic reflex (fig. 9 shows this with flexor muscles), but that on the other hand the stimuli may yet succeed in producing the rhythmic reflex when quite indubitably and markedly unequal in intensity, if that inequality does not go beyond certain limits.

Fig. 10 will serve as illustration. In this experiment the thresholds of r. and l. nerves lay at 19·5 and 20·5 respectively. The physical circuits were hardly appreciably unequal, for the thresholds changed only to 19·2 and 20·8 when the coils were interchanged for the two nerves by the double

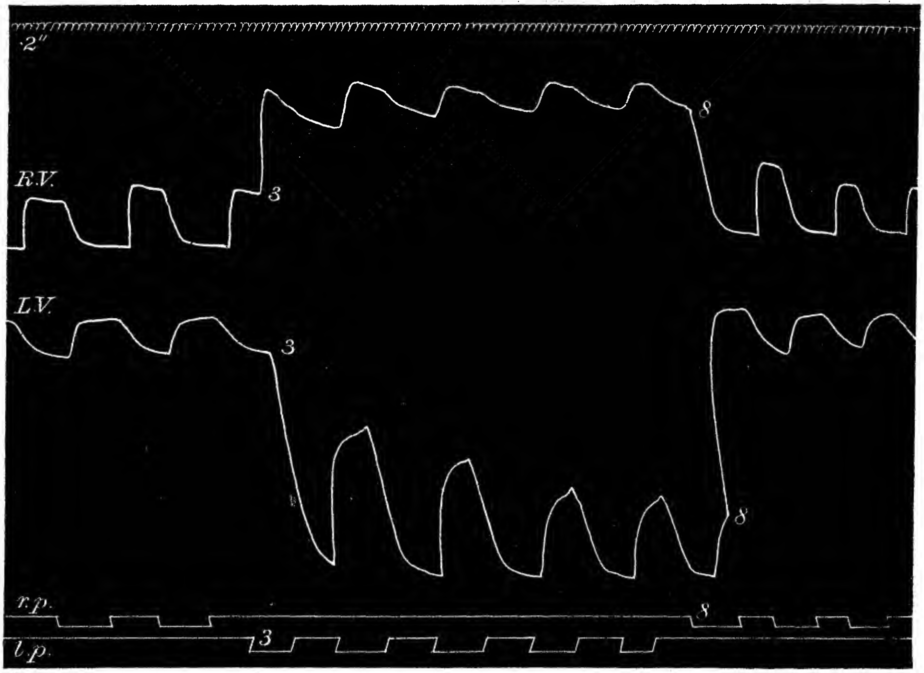

Fig. 11.—A series of reflexes, phasic and tonic, provoked in the isolated right and left vastocrureus muscles by short non-concurrent faradisations of right and left peroneal nerves. The numerals mark some salient corresponding events in the signal lines and myograms. The inhibitory relaxations produced in right vastocrureus, R.V., by stimulation of *r.p.* are followed by rebound contractions ; similarly the inhibitions of L.V. are followed by post-inhibitory rebounds on withdrawal of each stimulation of *l.p.*, left peroneal. Besides the reciprocal reflex movements induced by each stimulus, the stimuli cause assumption of reflex postures, *e.g.* under stimulation of *r.p.* the two myogram lines approach each other, *i.e.* r. muscle is relaxed (indicating that flexion of right leg would be going on, were the muscles not paralysed) and l. muscle is contracted (indicating that left limb would be extended). Under stimulation of *l.p.* the two myograph levers diverge, indicating that left limb assumes posture of flexion and right limb that of extension. This figure gives the separate effects of the two stimuli which, when concurrent, give the stepping reflex recorded in fig. 1. Decerebrate cat. Time in fifths of seconds.

switch. This being so we must consider the stimuli r. 13 and l. 16 distinctly unequal. Their separate effects on the preparation are shown at the beginning of fig. 10. It is noticeable there that the rebound contraction after the inhibition produced by r. 13 is greater than after that produced by l. 16; also that r.'s contractive effect on L muscle is better maintained than is l.'s on R muscle. Yet this combination produces, as the figure shows, good stepping in one of the muscles. Now this fig. 10 is from the same experiment as furnished fig. 1 and the combined stimuli in fig. 1 are $\frac{\text{r. 14}}{\text{l. 17}}$. And $\frac{\text{r. 13}}{\text{l. 16}}$ must be considered less equal than $\frac{\text{r. 14}}{\text{l. 17}}$, yet the rhythmic stepping of the left muscle in fig. 10 is as good or better than that in fig. 1. Now the stimuli used in fig. 1 were themselves unequal, not merely on the face of their scale values but as tested on the preparation at the time. Fig. 11 shows the effects of these two stimuli when employed separately; the tonic effect is obviously not equal but also not far from equal; but (fig. 12) the rebound is greater after inhibition

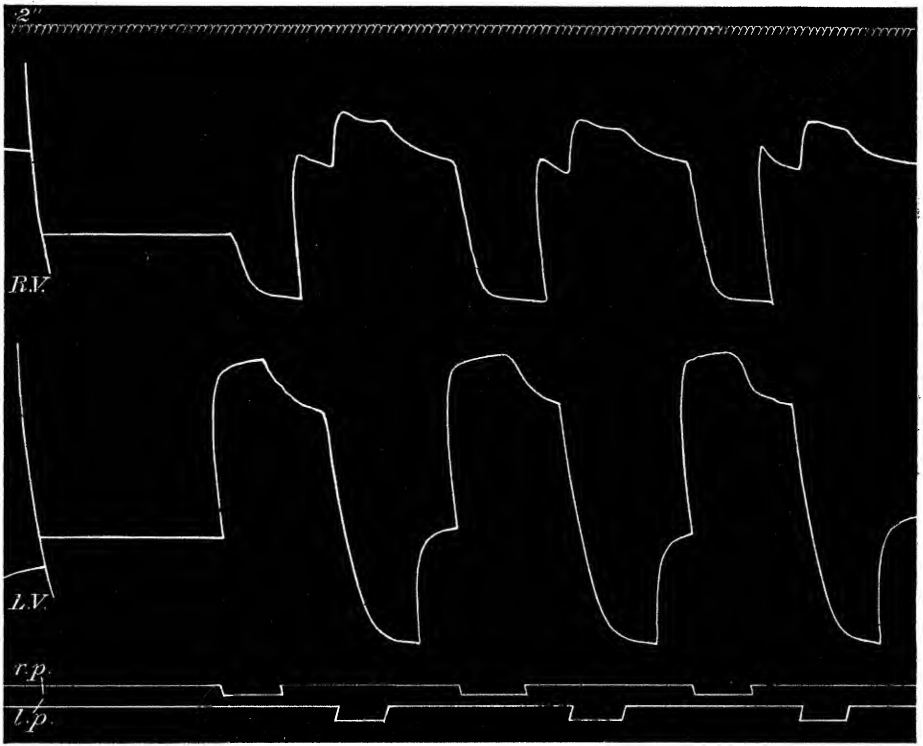

Fig. 12.—Right knee extensor (R.V.) and left (L.V.) isolated and reacting reciprocally to reflex stimulation of each peroneal afferent; *r.p.*, right peroneal, *l.p.*, left peroneal. Time above in fifths of seconds. Decerebrate cat.

by r. 14 than after inhibition by l. 17. And when, in fig. 13, the r. and l. stimuli are applied synchronously (observation 50) and begin together, r. stimulus obviously has the upper hand, for L muscle at once contracts, and though not seen in the figure R muscle at once relaxed. Moreover on withdrawing the two stimuli together L muscle at once relaxes instead of showing rebound contraction. Clearly r. stimulus is stronger than l. stimulus in its effect on the preparation. Observations 50, 51, 52, 54, fig. 12, in which r. and l. stimuli are applied together, do not differ in result on the muscle from observations 48 and 49, fig. 12, in which r. stimulus was applied alone, except in the feature that some little while after commencement of each of the double stimulations (observations 50–54) an inhibitory notch appears in the reflex contraction, whereas in observations 48 and 49 there is nothing of the kind. Reserving this point of difference for the present, the result here is that of the two stimuli r. 14 and l. 17 the former is the stronger not only in its numerical scale-value but also as actually tested on the preparation. Yet this pair of unequal stimuli give a good rhythmic reflex during their concurrent application (figs. 1 and 13). If r. 14 and l. 17 form an unequal pair in which r. is the stronger, obviously r. 13 and l. 16 must form a pair more unequal still. Yet $\frac{\text{r. } 13}{\text{l. } 16}$ gives a good rhythmic reflex in one of the muscles (fig. 13).

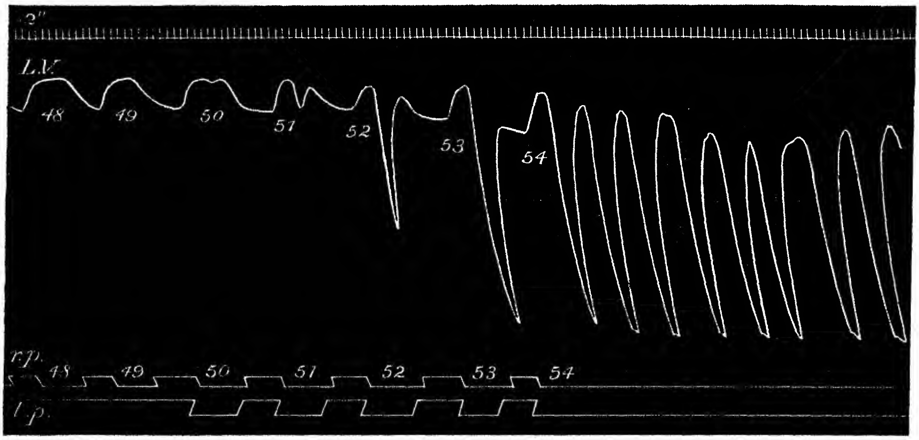

Fig. 13.—Extensor muscle of left knee L.V. Observations 49 and 50 show reflex contractions evoked by stimulation of right peroneal nerve, *r.p.* Then 50–54, a series of synchronous stimulations of *r.p.* and *l.p.*; during these there ensues stepping; the inhibitory phase (flexion phase) of the step appears as a gradually increasing inhibitory notch on the contraction caused by *r.p.* Time above in fifths of seconds.

Certainly, therefore, in order to produce the rhythmic reflex, the two antagonistic stimuli, right and left, need not be exactly equally balanced but experience points to the necessity of their being not widely unequal, also to the need for closer balance of r. and l. stimuli for evoking bilateral rhythmic reflex than for evoking a unilateral one.

Results referred to at the outset of this communication throw some light on this. It was there said that as the intensity of stimulus used for evoking the reciprocal reflex on the muscle pair is progressively increased, the intensity of both ipsilateral inhibition and contralateral contraction increase, but that of the former more rapidly than that of the latter. Synchronous application of r. and l. stimuli of equal strength produces when the stimuli are strong suppression of contraction both r. and l.; but with weak stimuli bilateral contraction, contraction of both muscles, results. The same result is shown by determining the strength of contralateral stimulus required to force its reflex contraction through an already established ipsilateral inhibition. The kind of result then met with is as follows: A preparation where threshold for r. peroneal was 16·4 cm., and that for l. peroneal 15·2 cm., yielded the figures—

	cm.		cm.
Inhibition of R. muscle by r. stim.	13	was broken by reflex contract. due to l. stim.	14
" "	12	" " "	12·5
" "	11	required l. 10 cm. to break it through.	
" "	10·5	" l. 9 " "	

Such results indicate a relation between intensity of stimulus and intensities of ipsilateral and contralateral reflexes such as is sketched in the diagram. The diagram accounts for the relation between the observations of

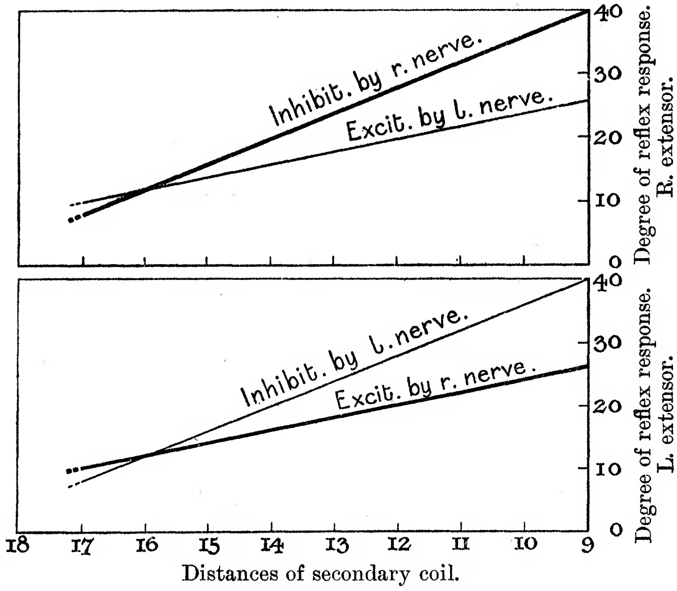

fig. 4 and fig. 5, both from the same experiment; also for that between the observations of fig. 1 and fig. 10, both from the same experiment. As drawn, the diagram applies to extensors (of knee), but by reversing inhibition to excitation and conversely it is applicable to flexors (of hip and knee).

4. *Influence of the Sequence.*

It is noticeable that the effect of concurrence of the stimuli opens with a result in the direction of that of the added stimulus practically at once on addition of that stimulus. Under the concurrence the newer stimulus tends to dominate at once. This is in harmony with experience on visual rivalry, struggle between rival contours, etc. The very newness of the new stimulus lends it force as against the pre-existent, especially where the pre-existent is not very much the more potent and has been in operation for some time.

Probably a similar relation explains why although well-acting combinations of the antagonist stimuli produce the rhythmic reflex whichever of the two stimuli precedes, with less effective pairs of stimuli that is not the case. It appears with the latter a point material for the result which of the two precedes and which follows (fig. 2). The rhythmic reflex may be much better if x precede y than *vice versâ*, or it may not appear at all in one sequence

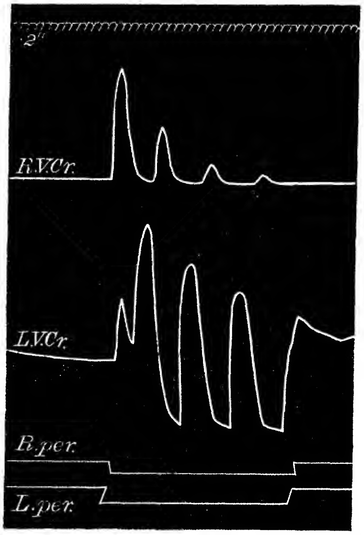

Fig. 14.—Isolated extensor muscle of right R.V. and left L.V. knees. Synchronous stimulation of both right and left peroneal afferents (*R. per.*), (*L. per.*) The reflex opens with identical contraction of both the muscles, but almost immediately the reaction of the left muscle is changed to inhibitory relaxation, with the result that the symmetrical muscles fall into step with reciprocal harmony. Decerebrate cat. Time above in fifths of seconds.

though appearing with the other. A particular combination which works need not necessarily work reversed, though it generally does so.

As to what happens when the two rival stimuli are started together, the observations have shown that sometimes then the reflex step starts at once with full reciprocity of phase in the two muscles, and so proceeds co-ordinately in that manner. Sometimes, however (fig. 14), the muscular effect begins identically with contraction in the two muscles, and this is almost immediately checked and reversed in one of the muscles so that that muscle then begins, although a little late, to behave reciprocally in regard to its fellow. In fig. 14 this correction takes place in time for L. muscle, although starting wrongly, to have got into harmonious reciprocal step with its fellow before even the completion of the first phase of the first step is reached. Harmonious reciprocity then continues.

When the two rival stimuli are started together there seems a tendency for the stronger to overcome the weaker altogether at first, and then to give way to the latter a little later, and then later still to re-establish ascendancy, again soon losing it, and so on. Thus a see-saw alternation of dominance is arrived at. Observation 54 in fig. 13 exemplifies this. The weaker stimulus (*v. supra*) l. 17 there makes its effect felt as a deep inhibition of a contraction already initiated by r. 14. And in the series of immediately precedent observations 50—53, this effect of l. 17 is seen to have each time occurred with the same time-relations, although with successively increasing effect. Evidence in the same direction is illustrated in fig. 7A.

5. *Influence of the Afferent Nerve of the Reacting Muscle.*

The rhythmic effect of the antagonistic concurrent stimuli takes place when the reacting muscle has been de-afferented. The presence of the proprioceptive afferents of the muscle is therefore not necessary to the reaction. Fig. 15 shows the rhythmic stepping obtained from the right vastocrureus by concurrent stimulation of the antagonistic r. and l. popliteal nerves. (The signals in this experiment were set to mark upwards, not downwards as in the other figures of this paper.) The observation begins with faradisation of r. nerve producing, after the initial spike (*Anfangstetanus*), inhibition; but the muscle being already relaxed, the preparation being decapitate, the inhibition causes no visible further elongation of its muscle, except the suppression of the initial contraction which it itself had provoked. After 2·5 secs. the stimulation of the contralateral popliteal is commenced, the stimulation of ipsilateral proceeding unaltered. The result of concurrence of the stimuli is immediate rhythmic stepping of the muscle. Four steps are taken during the continuance of the concurrent

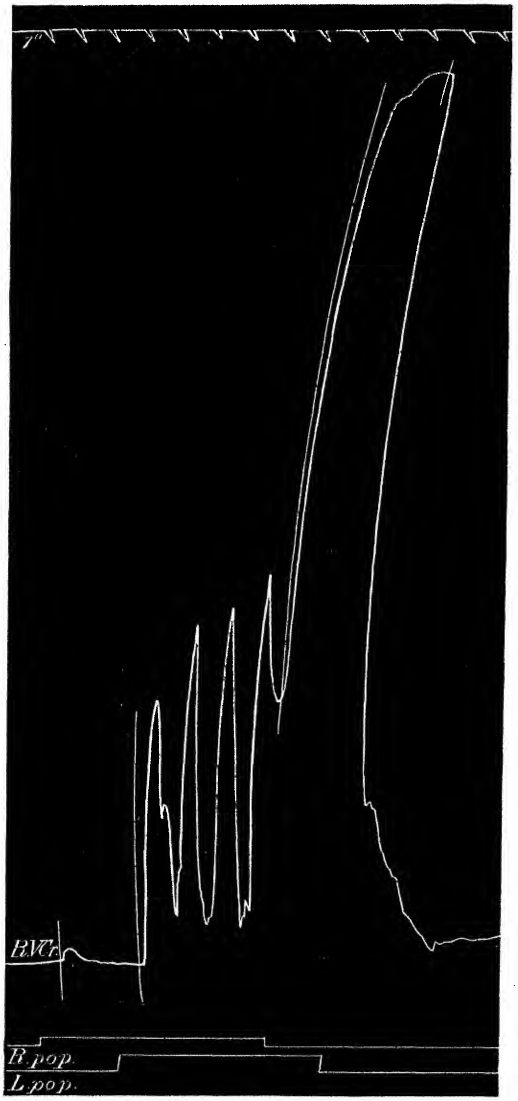

Fig. 15.—Isolated de-afferented extensor muscle of right knee. Decapitate cat. Faradisation of central end of right popliteal nerve for 6·5 secs., joined 2·2 secs. after its commencement by faradisation of left popliteal nerve ; the latter stimulation is continued until 2 secs. after cessation of right popliteal stimulation. The signal marks are directed upward instead of downward as in the other records. During the concurrence of the stimuli, but not when either of the two stimuli is in operation alone, the muscle gives rhythmic reflex stepping ; it completes four steps in about 4 secs. The muscle had been de-afferented (118 days). The proprioceptive reflex—"shortening reaction"—is therefore absent on withdrawal of the contralateral stimulus, and the muscle relaxes at once, being toneless. Time above in seconds.

stimulation, *i.e.*, in 4·5 secs.; the ipsilateral stimulus is then withdrawn, and under the influence of the remaining contralateral stimulus the muscle enters at once into steady maintained contraction, and continues so contracted until the stimulus is withdrawn. The muscle had been de-afferented October 7, 1908, and was used for experiment nearly four months later, February 2, 1909. In the experiments of Graham Brown* it has been shown that stepping occurs after de-afferenting the muscles involved.

6. *Influence of a Component Stimulus subsequent to its Withdrawal.*

In the rhythmic reflex a contraction-phase (extension-phase of step) which is in course of execution does not cease immediately on withdrawal of the contralateral stimulus. On the contrary it continues its course for a brief time and ends in smooth transition and reversal into relaxation. This want of abruptness is strikingly different from the abruptness with which a reflex inhibition excited by an ordinary stimulus against tonus often commences. The excitatory phase thus continued after withdrawal of the contralateral stimulus is frequently less ample than its predecessors where the stimulus was not withdrawn (fig. 16, observation 2). A small final step to the series is thus produced (fig. 1, observation 1). If the contralateral stimulus be withdrawn during the course of the relaxation phase of the rhythmic reflex, *i.e.* during the flexion phase of the step, often no subsequent contraction-phase ensues (fig. 4, observations 3 and 4), even although the withdrawal occur late in the course of the relaxation phase (fig. 4, observation 3). But if the contralateral stimulus be relatively strong and the ipsilateral relatively weak, and the former be withdrawn just before the end of the relaxation phase, a small and somewhat delayed subsequent contraction phase may ensue (fig. 10, observation 3), and even be followed by one still smaller and still more delayed (fig. 1, observation 3).

Conversely with the withdrawal of the ipsilateral stimulus. If this cease during a relaxation phase that phase is completed more or less amply after the stimulus withdrawal (fig. 4, observation 1). If it be withdrawn during a contraction-phase no relaxation phase usually follows, but there may be just the commencement of one if the ipsilateral stimulus is withdrawn at end of a contraction phase (fig. 16, observation 1), and if the ipsilateral stimulus as compared with contralateral be not too weak.

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* 'Roy. Soc. Proc.,' 1911, B, vol. 84, p. 308.

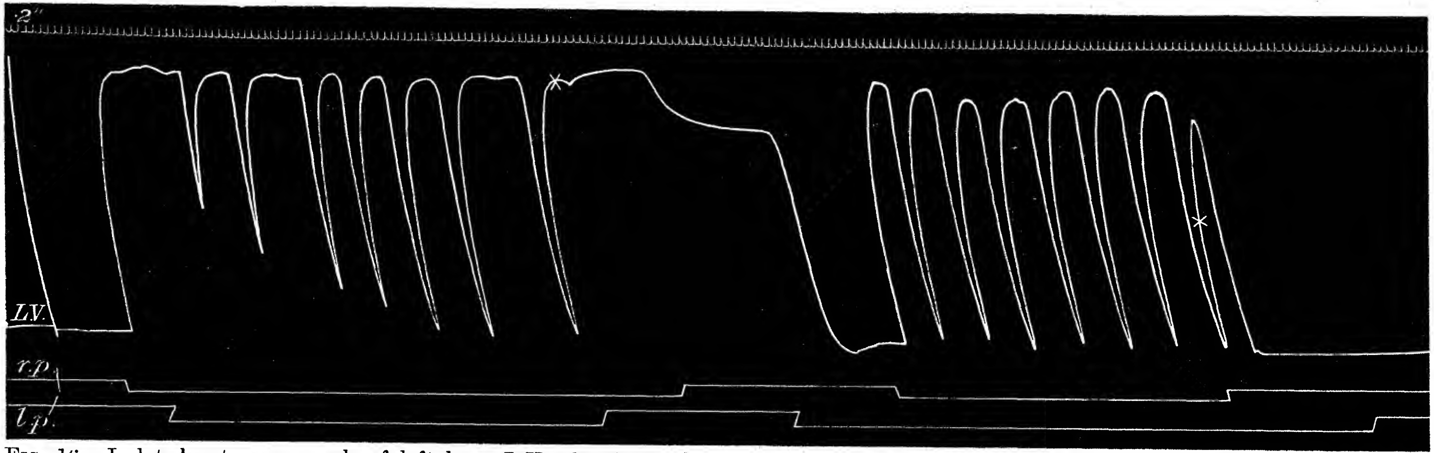

Fig. 16.—Isolated extensor muscle of left knee L.V., showing reflex stepping produced by concurrent stimulation of the right and left peroneal afferents, *r.p.* and *l.p.* The figure shows that one and the same stimulus combination does not work equally well on two successive occasions. In Observation 1 the figure illustrates the after-effect of the inhibitory stimulus subsequent to its withdrawal, its effect being the small notch occurring just after the cross. In Observation 2 the dwarfing of the contraction (extensor) phase after withdrawal of the excitatory stimulus just previously is shown. The moment of withdrawal of the stimulus is marked by a cross. Decerebrate cat. Time above in fifths of seconds.

IV. SUMMARY OF CONCLUSIONS.

It is shown that taking an afferent nerve which produces steady reflex excitation of the muscle, and another which produces steady reflex inhibition of the muscle, it is possible by stimulating both nerves concurrently to obtain regularly rhythmic contractions and relaxations of each member of a pair of symmetrical muscles, the phases being reciprocal in the two. To do this requires certain somewhat narrowly adjusted proportions of strength of the two paired stimuli. The stimuli are both of them continuous, in the sense that they are faradic and of a frequency (about 40 per second) much above and bearing no causal relation to the rhythmic reflex produced. In the rhythmic reflex the right and left muscles each contract and relax alternately and move reciprocally, the contracting phase of right muscle being synchronous with the relaxing phase of left, and conversely. This rhythmic reflex is shown clearly to be reflex stepping. In short, under the rivalry of the two opposed and so to say equipoised continuous stimulations the limbs exhibit reflex walking. With certain other paired intensities of stimulation of the two antagonistic afferent nerves, it can be arranged that only one muscle of the pair shall step—the left muscle if the right nerve stimulus be the stronger, and conversely. During this unilateral walking or running the other leg is kept steadily flexed by the reflex, *i.e.* the extensor muscles are kept steadily inhibited.